

Convergence, Divergence, and Homogenization in the Ecological Structure of Emydid Turtle Communities: The Effects of Phylogeny and Dispersal

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ABSTRACT: Studies that have explored the origins of patterns of community structure from a phylogenetic perspective have generally found either convergence (similarity) in community structure between regions through adaptive evolution or lack of convergence (dissimilarity) due to phylogenetic conservatism in the divergent ecological characteristics of lineages inhabiting different regions. We used a phylogenetic approach to document a third pattern in the structure of emydid turtle communities. Emydid communities in southeastern North America tend to have a higher proportion of aquatic species than those in the northeast. This pattern reflects phylogenetic conservatism in the ecology and biogeography of two basal emydid clades, limiting convergence in community structure between these regions. However, differences in community structure between northeastern and southeastern North America have also been homogenized considerably by the dispersal of species with phylogenetically conserved ecological characteristics between regions. This pattern of ecologically conservative dispersal may be important in many continental and oceanic systems.

Keywords: biogeography, community ecology, community structure, convergence, dispersal, Emydidae.

The ecological structure of communities has only rarely been explored from a phylogenetic perspective (reviewed in Losos 1996; Webb et al. 2002). However, community structure is determined by the traits of species, and these traits ultimately arise via evolutionary processes. By com-

munity structure, we mean the number of species of each ecological type or guild in a natural community (e.g., number of sympatric carnivorous, omnivorous, and herbivorous species; see Roughgarden and Diamond 1986 for a review of terminology). In general, the structure of a community should be determined by adaptive evolution of species to conditions within the community (including coexisting species); immigration of species into the community, each having a given set of ecological characteristics; local extinction of species; and the age of the community and thus the amount of time for adaptation, immigration, and extinction to occur (modified from Brooks and McLennan 1991; Losos 1996). The adaptive evolution of species to local conditions will tend to be limited by the time frame over which adaptation can occur and phylogenetic conservatism (also known as phylogenetic inertia or niche conservatism). We define phylogenetic conservatism as the tendency of species to retain the traits of their ancestors (Losos and Miles 1994), a pattern that can arise via many mechanisms (e.g., developmental or genetic constraint, stabilizing selection; reviewed in Schlichting and Pigliucci 1998). A thorough understanding of the processes that determine community structure requires a phylogenetic perspective.

Several pioneering studies have recently explored the relationship between the phylogenetic history of lineages and patterns of community structure (e.g., Losos 1990, 1992; Winemiller 1991; Gorman 1992; Richman and Price 1992; Cadle and Greene 1993; Hertel 1994; Richman 1996; Radtkey et al. 1997; Losos et al. 1998; McPeck and Brown 2000; Price et al. 2000). These studies have generally found one of two patterns (fig. 1): convergence in community structure between regions through adaptive evolution (i.e., the independent evolution of species with similar ecological characteristics in similar environments in different regions; Schluter 1986; Pianka 2000) or lack of convergence due to phylogenetic conservatism in the dissimilar ecological characteristics of lineages inhabiting each region. Several studies (e.g., Winemiller 1991; Losos 1992;

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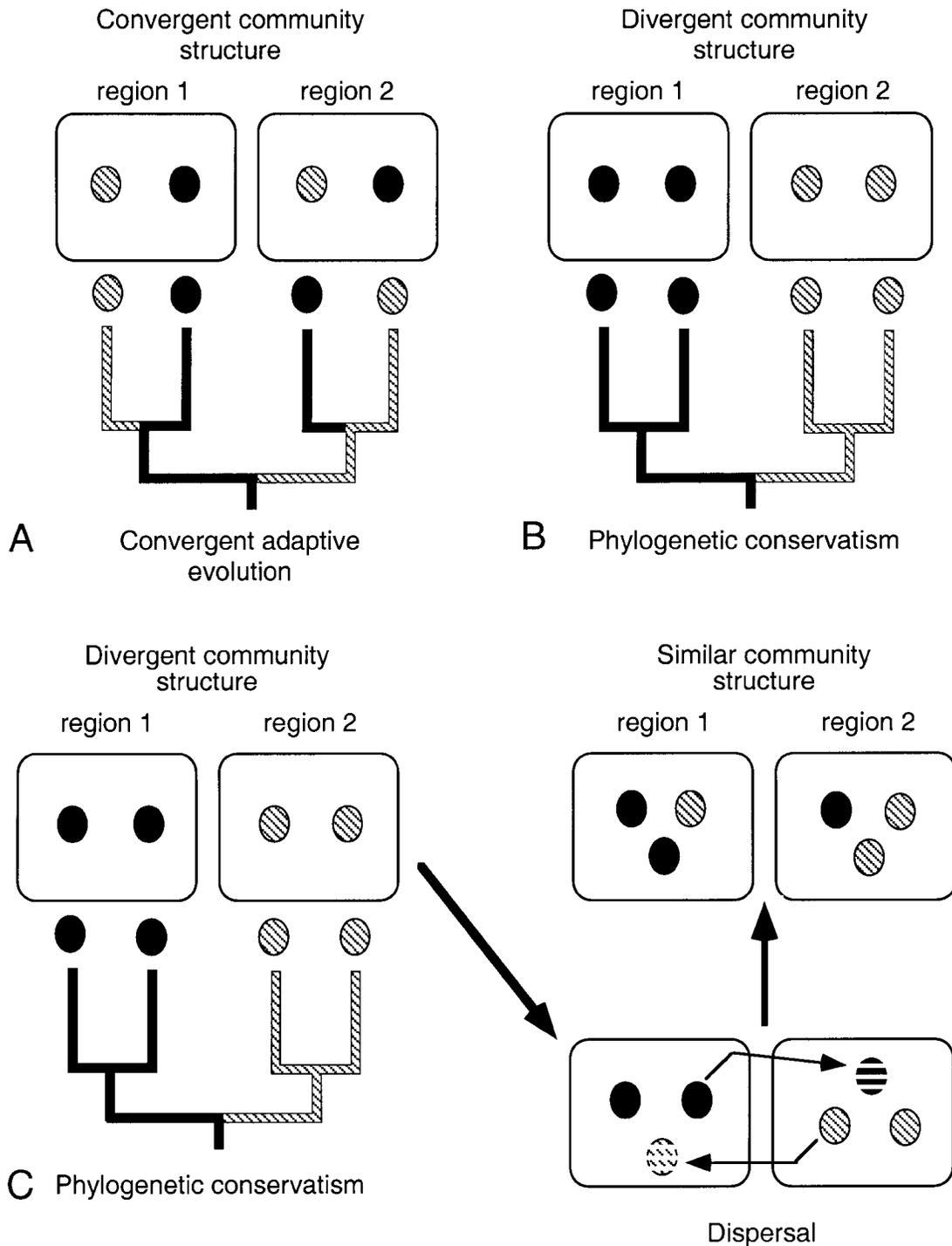


Figure 1: Hypothetical examples showing (A) adaptive evolution causing convergence in community structure between regions, (B) phylogenetic conservatism in ecological traits preventing convergence in community structure between regions, and (C) how ecologically conservative dispersal can homogenize community structure between regions. The circles within each box represent species within communities of a given region. Shading represents the ecological characteristics of species. In both A and B, lineages inhabiting communities in different regions (*region 1* and *region 2*) initially have differing ecological characteristics. In A, species with identical ecological characteristics evolve in both regions, leading to convergence in the ecological structure of communities between regions. In B, strong phylogenetic conservatism in the ecological characteristics of the lineages prevents convergent adaptive evolution in the two lineages. Thus, the ecological structure of communities in *region 1* differs from that in *region 2*. In C, phylogenetic conservatism in the ecological characteristics of lineages leads to differences in the ecological structure of communities in *regions 1* and *2* (left). However, if some species with conserved ecological characteristics are able to disperse between regions (small arrows, lower right), patterns of ecological structure between regions will be homogenized (upper right).

Hertel 1994; Losos et al. 1998) have found that communities in similar environments can converge in structure (fig. 1A). For example, Losos et al. (1998) showed that the same set of habitat specialists has evolved repeatedly and independently among *Anolis* lizards on different islands in the Greater Antilles. In this case, the ecological characteristics of species are determined more by the preexisting community structure (i.e., the available niche space) than by the phylogenetic history of lineages. Other studies have found that phylogenetic trends (conservatism) in ecological characters and distribution of lineages can restrict the structure of communities within a given region and prevent convergence between regions (fig. 1B; e.g., Gorman 1992; Cadle and Greene 1993; Price et al. 2000). Cadle and Greene (1993) found that ecological equivalents rarely evolved independently in separate clades of Neotropical snakes and that the ecological structure of communities in a region could be constrained by the presence or absence of particular clades. For example, certain guilds in South American communities, such as fossorial species that prey primarily on other snakes, have no ecological equivalents in Central American communities.

Dispersal may also be an important process in determining patterns of community structure between regions. The dispersal of species or clades with phylogenetically conserved ecological characteristics (ecologically conservative dispersal) can contribute to homogenization of community structure between different regions (fig. 1C). This pattern has only rarely been sought or documented (e.g., Losos 1992; Brooks and McLennan 1993). Previous phylogenetic studies of community structure have generally focused on relatively isolated communities, such as islands (e.g., Losos 1990, 1992; Losos et al. 1998), glacial lakes (e.g., Bernatchez et al. 1999), or those in geographically distant continental regions (e.g., Richman 1996; Price et al. 2000). The homogenizing effects of dispersal on geographic patterns of community structure may be greatly diminished in such cases. A further limitation of past phylogenetic studies of community structure is that few have examined more than a handful of communities (e.g., Losos 1992; Cadle and Greene 1993; McPeck and Brown 2000; Vitt et al. 2003), and of these only two examined an ecologically diverse group (i.e., one that includes a wide range of habitat and dietary specialists; Cadle and Greene 1993; Vitt et al. 2003).

In this study, we examine the effects of evolutionary history and dispersal on patterns of community structure in a geographically widespread and ecologically diverse group of vertebrates, emydid turtles. Emydids are an excellent study group because the ecology and geographic distribution of individual species are relatively well known (Ernst and Barbour 1989; Ernst et al. 1994), and a detailed species-level phylogenetic hypothesis is available (Stephens

and Wiens 2003a). Emydidae currently contains 40 species (Ernst and Barbour 1989; Ernst et al. 1994; Vanzolini 1995; Stephens and Wiens 2003a; but see Seidel 2002) and 12 genera (Holman and Fritz 2001; Feldman and Parham 2002). These genera are divided into the subfamilies Emydinae (*Actinemys*, *Glyptemys*, *Clemmys*, *Emydoidea*, *Emys*, and *Terrapene*; Crother et al. 2003) and Deirochelyinae (*Chrysemys*, *Deirochelys*, *Graptemys*, *Malaclemys*, *Pseudemys*, and *Trachemys*; Gaffney and Meylan 1988). Members of the family are found in Europe, North America, Middle America, the West Indies, and South America, but the majority of species occurs in eastern North America (Iverson 1992). Emydids are ecologically diverse and include generalists and specialists in both habitat (including terrestrial, semiterrestrial, and aquatic species) and diet (including herbivores, omnivores, and carnivores; Ernst et al. 1994).

For the first time in a phylogenetic study of community structure, we combine a comprehensive phylogeny for a speciose, ecologically diverse lineage with data on communities representing nearly every unique assemblage of species within the group ($n = 74$). We find that the lack of convergence in the structure of communities between regions in eastern North America is related to phylogenetic conservatism in the ecological traits of the two basal emydid lineages. However, we also find that dispersal of lineages with phylogenetically conserved ecological traits (ecologically conservative dispersal) has caused considerable homogenization of the structure of communities throughout the range of Emydidae.

Material and Methods

A detailed description and justification of methods is given in appendix A in the online edition of the *American Naturalist*. Our methods are only briefly outlined here. The phylogeny used in this study was based on a combined analysis of morphological data and mitochondrial sequence data that included nearly all currently recognized species of emydids (Stephens and Wiens 2003a, their fig. 7).

Ecological characters (habitat and diet) were reconstructed on the tree both as discrete characters (using parsimony) and as continuous characters (using maximum likelihood). Habitat and diet are the primary axes along which turtles divide ecospace (Bury 1979; Vogt and Guzman 1988; Lindeman 2000). Characters were scored for each species on the basis of literature surveys (Smith and Smith 1979; Seidel 1988; Ernst and Barbour 1989; Ernst et al. 1994). Parsimony reconstructions of discrete character states were performed using MacClade, version 4.0 (Maddison and Maddison 2000). For diet, each species was coded as a carnivore (0), omnivore (1), or herbivore

(2). For habitat use, each species was coded as aquatic (0), semiterrestrial (1), or terrestrial (2). Admittedly, the ecological character states used were quite broad and could mask important variation between or within species. However, many emydid species exhibit considerable geographic, seasonal, and sexual variation in their ecological habits (Ernst et al. 1994), and more detailed species-level designations could not have been applied consistently. Regardless, these broad categories clearly represent dramatic extremes in ecological specialization. Maximum likelihood (Schluter et al. 1997) reconstructions of quantitative trait values were performed using COMPARE, version 4.5 (Martins 2001).

Tests of phylogenetic conservatism in ecological characters and geographic distribution of lineages were performed on the combined-data tree using the method of Maddison and Slatkin (1991). Character states were randomly shuffled among taxa 1,000 times using MacClade.

The ecological structure of emydid communities was determined by combining data on the ecological attributes of species with data on their geographic distributions. We consider emydid community to mean all species of emydids that co-occur at a particular place (we also use "assemblage" interchangeably with community in this sense). Drainages and islands form natural geographic divisions for emydid turtles because the majority of species are dependent on freshwater habitats. River drainages and islands were therefore used as a starting point to identify all unique assemblages of emydid turtles (i.e., each unique combination of coexisting species). For each drainage or island ($n = 74$), species composition was tabulated at a single geographic point where the maximum number of species overlapped on the basis of geographic references listed above. In theory, we could have estimated community structure on the basis of species present in a given habitat or locality (e.g., a particular pond or field). However, the appropriate scale for examining community structure is organism specific (Morin 1999), and such a small scale would not be appropriate for emydids. Many emydid species forage over wide areas in different times of the year, in some cases moving between aquatic and terrestrial habitats (e.g., Rowe and Moll 1991; Kaufman 1992; reviewed in Ernst et al. 1994). Because individuals may occur in very different habitat types, this landscape-scale approach for estimating community structure is more reasonable for emydids than considering only a single habitat type or types.

Preliminary analyses suggested that there are differences in the taxonomic composition and ecological structure of emydid communities between southeastern and northeastern North America. Assemblages in northeastern North America seem to contain more emydines but fewer deirochelyines than do southeastern communities. Emy-

dines in eastern North America are generally omnivores and are terrestrial or semiterrestrial, whereas deirochelyines are all aquatic and are more frequently specialized in diet (including fewer omnivores). Because of these phylogenetic trends, we expected communities in northeastern North America to contain more omnivorous (emydine) species but fewer aquatic (deirochelyine) species compared with those in southeastern North America. In order to objectively quantify these latitudinal trends, data from assemblages in eastern North America were used in a series of linear regression analyses performed using Statview, version 4.1 (Roth et al. 1992).

Despite the apparent overall dominance of the northeast by emydines and the southeast by deirochelyines, there are a number of species that are very widely distributed and that seem to blur these trends. If geographic patterns of community structure were homogenized by ecologically conservative dispersal (i.e., fig. 1C), we would expect that geographic differences in community structure should become stronger if widespread species are excluded; broadly distributed deirochelyine species are widespread in northern communities and broadly distributed emydines are widespread in southern communities; and deirochelyines that are widespread in northern communities are derived from more southern ancestors and emydines widespread in southern communities are derived from more northern ancestors. The first expectation was tested by removing widespread species (i.e., those that occurred in more than 20% of emydid communities, $n = 10$ species of 29 total) from community totals and repeating regression analyses. The second expectation was tested by tabulating the percentage of northeastern and southeastern communities in which each of the 10 widespread species occurs to see whether widespread deirochelyine species occur in a large percentage (i.e., >20%) of northeastern communities and to see whether widespread emydid species occur in a large percentage of southeastern communities. The third expectation was tested by reconstructing the latitudinal midpoint of the ranges of all hypothetical emydid ancestors using continuous maximum likelihood. A major assumption of this analysis is that the ranges of species have remained relatively stable over time and that shifts in latitudinal midpoints are indicative of the general direction of dispersal. The fossil record suggests some species experienced dramatic range shifts during the Pleistocene (Holman 1995). Unfortunately, the fossil record for emydids is inadequate to allow ancestral distributions to be assessed more directly.

Latitudinal midpoints were reconstructed and standard errors were calculated using COMPARE, version 4.5 (Martins 1999). Confidence intervals for reconstructed values were calculated from the standard errors using the method of Schluter et al. (1997). Martins (1999) has shown that

such confidence intervals are essentially meaningless because the standard errors that they are based on will tend to overestimate or underestimate the accuracy of reconstructions in a way that is hard to predict. These confidence intervals are also often wider than the total range of values observed among the tip taxa (Schluter et al. 1997; Garland et al. 1999; Polly 2001). The results of our analysis also highlight these limitations (table 1). The confidence interval for the latitudinal midpoint of the ancestors of several taxa spans more than 15° latitude, which is wider than the total latitudinal range of all but a few modern emydid species.

Despite the inability of current methods to accurately estimate uncertainty, both simulation (Martins 1999) and empirical studies (Polly 2001) have shown that values reconstructed using maximum likelihood are generally reasonably accurate approximations of the values that they estimate. Given that there is an unknown level of uncertainty around each reconstructed latitudinal midpoint, we limit our interpretation of these midpoints to the observation that reconstructed latitudinal midpoints represent the most likely position of the ancestor in comparison to the descendant taxa (i.e., north of it or south of it), or they represent the continental region (i.e., northeastern North America, southeastern North America) in which an ancestor is most likely to have occurred. Such a broad interpretation of these results is well justified by studies

of reconstructed ancestral values (Martins 1999; Polly 2001). We do not claim that these results should be considered statistically significant and allow that future methodological refinements or sources of data (e.g., fossil evidence, intraspecific phylogeographic studies) could easily overturn the results of these reconstructions.

Results

Mapping ecological characters onto the phylogeny using parsimony and likelihood gave similar results. Both methods revealed major differences between the two emydid subfamilies in their patterns of ecological diversification (fig. 2; Stephens and Wiens 2003a). Deirochelyinae includes herbivorous, omnivorous, and carnivorous species that are all aquatic. In contrast, most emydines are omnivorous, and the subfamily includes aquatic, semiterrestrial, and terrestrial species. Thus, deirochelyines have remained conservative in habitat but have diversified in diet whereas emydines have remained conservative in diet but have diversified in habitat use (Stephens and Wiens 2003a). Both diet and habitat showed highly significant phylogenetic conservatism ($P < .001$), as did geographic distribution ($P < .001$). In eastern North America, all deirochelyine species and clades are restricted to southeastern North America or else occur in both southeastern and northeastern North America. Conversely, all species of

Table 1: Trends in the geographic distribution of emydid species (and their ancestors) that are widespread in eastern North America

Taxon	Southeastern assemblages inhabited (%)	Northeastern assemblages inhabited (%)	Latitudinal midpoint of geographic range (°)	Reconstructed latitudinal midpoint of ancestor (°)
<i>Chrysemys picta</i>	56	100	40.4	33.1 ± 7.6
<i>Deirochelys reticularia</i>	64	0	31.2	32.3 ± 7.6
<i>Graptemys ouachitensis ouachitensis</i>	28	36	37.0	35.3 ± 5.4
<i>Graptemys pseudogeographica</i>	28	32	37.9	35.3 ± 5.4
<i>Graptemys geographica</i>	20	68	39.9	35.0 ± 6.0
<i>Pseudemys concinna</i>	68	18	34.5	32.9 ± 5.3
<i>Trachemys scripta</i>	84	46	33.6	29.3 ± 6.3
<i>Clemmys guttata</i>	16	36	37.5	37.1 ± 7.0
<i>Terrapene carolina</i>	88	68	34.7 ^a	27.8 ± 6.0 ^a
<i>Terrapene ornata</i>	40	36	34.9	28.4 ± 6.7
Deirochelyinae	100	100	10.0	32.3 ± 7.6
Emydinae	100	100	33.2	32.8 ± 8.0
[<i>Terrapene</i>]	100	90	31.3	26.1 ± 7.1
[<i>Actinemys</i> + <i>Glyptemys</i> + <i>Clemmys</i> + <i>Emys</i> + <i>Emydoidea</i>]	20	63	38.3	37.1 ± 7.0

Note: Assemblages in eastern North America were classified as northeastern or southeastern in relation to 37.5° north latitude. The seven species in boldface are the ones that occur in at least 20% of both northeastern and southeastern assemblages and thus that have been most important in homogenizing patterns of community structure between regions. The values to the right of ± indicate 95% confidence intervals on the reconstructed latitudinal midpoints (but see caveats in “Material and Methods”). *Trachemys scripta* refers to only the eastern North American subspecies (i.e., *Trachemys scripta elegans*, *Trachemys scripta scripta*, and *Trachemys scripta troostii*).

^a These values are for a clade consisting of *Terrapene carolina* [*bauri* + *major* + *carolina*], the largest monophyletic group of *T. carolina* subspecies.

emydines in eastern North America are either restricted to the northeast or occur in both northeastern and southeastern North America.

Analysis of species composition and ecological structure of emydid communities showed four major trends (see app. B in the online edition of the *American Naturalist* for raw data). First, communities in eastern North America have many species (mean = 5.53, $n = 55$ assemblages) with varied ecological characteristics (most contain both aquatic and terrestrial species and both omnivorous and carnivorous species). Communities in other regions (western North America, Europe, Africa, the West Indies, and the Neotropics) have only one or two species (mean = 1.29, $n = 19$) and correspondingly reduced ecological diversity (see Stephens and Wiens 2003b for discussion of patterns of species richness in emydids). Thus, we focus further analyses on patterns in eastern North America. Second, within eastern North America, all emydid species are terrestrial or semiterrestrial, and all deirochelyines are aquatic. Third, communities in southeastern North America have more deirochelyine species than emydid species and thus tend to have more aquatic species and dietary specialists than those in northeastern North America. Conversely, communities in northeastern North America have more emydid species and therefore tend to have more semiterrestrial species and omnivores than those in southeastern North America (see below for quantitative analysis). Finally, several ($n = 10$) species that are distributed widely in eastern North America (i.e., occurring in both the southeast and the northeast) seem to blur these geographic patterns of community structure. For example, many southeastern communities contain the semiterrestrial and terrestrial emydines *Clemmys guttata* and *Terrapene carolina*, whereas many communities in the northeast contain the aquatic deirochelyines *Graptemys geographica* and *Chrysemys picta*.

Quantitative analysis of geographic trends in community structure and composition within eastern North America confirms the qualitative pattern described above and shows that the percentage of emydid species in eastern North American communities is positively correlated with latitude ($r^2 = 0.329$, $P < .001$; fig. 3); the percentage of aquatic species in communities is negatively correlated with latitude ($r^2 = 0.329$, $P < .001$; fig. 4A) and perfectly negatively correlated with the percentage of emydines ($r^2 = 1.000$; fig. 4B); and there is a significant positive correlation between the percentage of omnivorous species and community latitude ($r^2 = 0.140$, $P = .010$; fig. 4C), but this is not related to the percentage of emydines in communities ($r^2 = 0.027$, $P = .266$; fig. 4D).

Repeating these analyses after excluding species that occur in more than 20% of the communities in eastern North America suggests that these geographic trends have been

blurred considerably by species that are widely dispersed. When widely distributed species are excluded, the percentage of aquatic species in communities is more strongly negatively correlated with latitude ($r^2 = 0.805$ [$P < .001$] vs. $r^2 = 0.329$, including all species) and still perfectly negatively correlated with the percentage of emydid species in communities ($r^2 = 1.000$). Similarly, the percentage of omnivores in communities is more strongly correlated with latitude ($r^2 = 0.669$ [$P < .001$] vs. $r^2 = 0.140$, including all species) and also the percentage of emydid species in communities ($r^2 = 0.797$ [$P < .001$] vs. $r^2 = 0.027$, including all species). Note that communities at similar latitudes are expected to draw from similar species pools and thus violate the assumptions of regression analysis (Sokal and Rohlf 1995). However, these analyses were merely intended to quantify patterns, not establish causal relationships. The P values are presented solely for comparative purposes.

As predicted by the ecologically conservative dispersal hypothesis, the majority of widely distributed deirochelyines ($n = 5$ of 7 deirochelyine species) occur in >20% of northern assemblages, and the majority of the widely distributed emydid species occur in >20% of southeastern assemblages ($n = 2$ of 3 emydid species).

As predicted by the ecologically conservative dispersal hypothesis, phylogenetic reconstruction of the latitudinal midpoint of geographic ranges suggests that all of the deirochelyine species that are widespread in northern communities had immediate ancestors that were more southern in distribution and that Deirochelyinae ancestrally occurred in southeastern North America (table 1). These results support the hypothesis that geographic trends in community structure are blurred by northward dispersal of aquatic deirochelyines. Surprisingly, however, these analyses also suggest that the two emydid species that are widespread in the southeast (*Terrapene carolina* and *Terrapene ornata*) had ancestors that were more southern in distribution and that these two emydines may also have dispersed northward (opposite of our prediction). Ancestral reconstructions suggest that Emydinae occurred ancestrally in southeastern North America and consists of two monophyletic lineages with different ancestral patterns of geographic distribution. One clade (*Terrapene*) occurred ancestrally in southeastern North America (or perhaps even northern Mexico) and invaded northeastern North America relatively recently. The other clade (all other emydines, including *C. guttata*, *Emydoidea blandingii*, and *Glyptemys insculpta* in table 1) seems to have occurred ancestrally in central North America (far north of the reconstructed ancestors of Emydidae, Emydinae, and *Terrapene*) and has no living representatives that are widespread in southeastern North America. On the basis of the confidence intervals in table 1, few of these results are

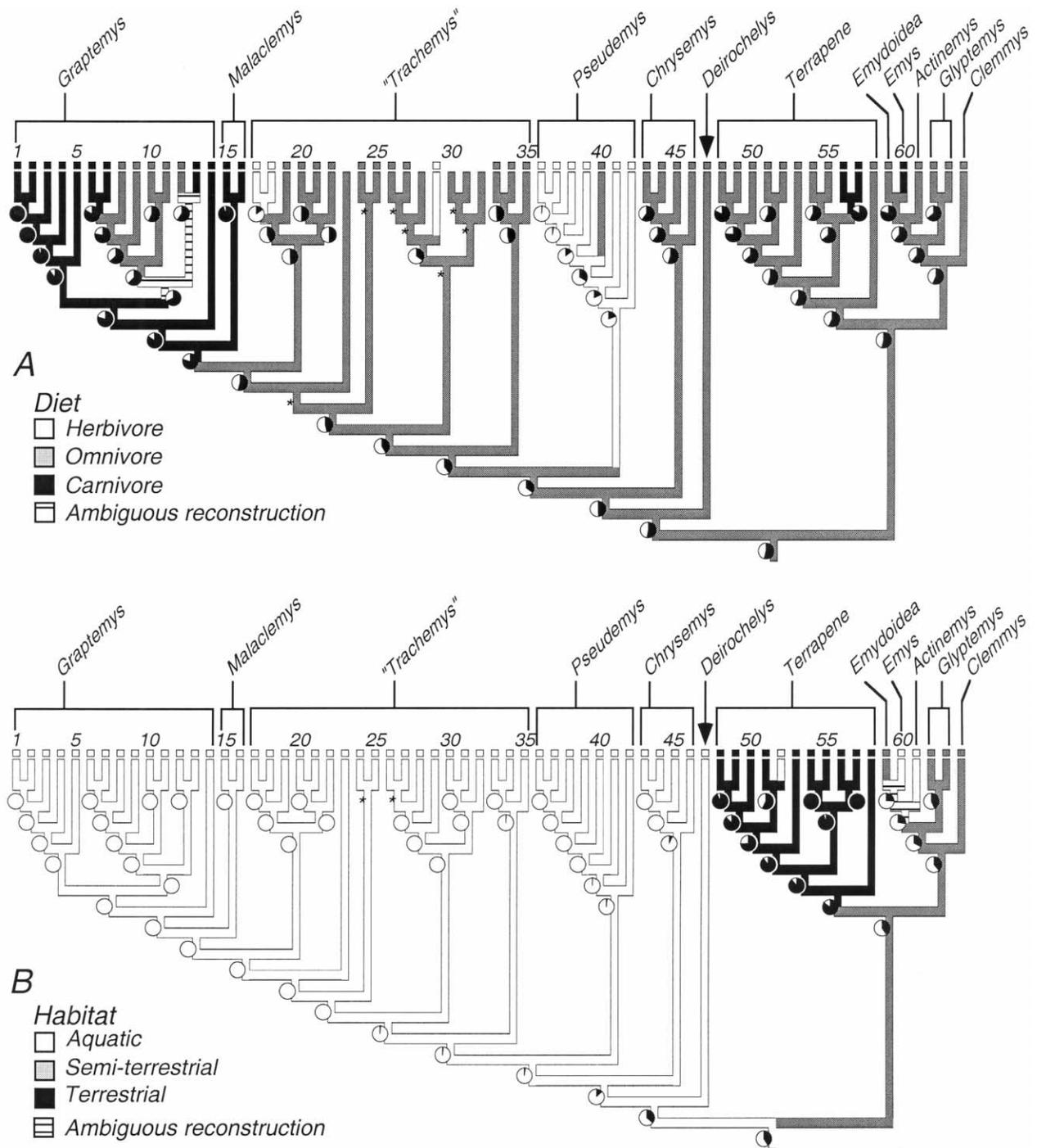


Figure 2: Ancestral reconstructions for (A) diet and (B) habitat use (modified from Stephens and Wiens 2003a) for all emydids. The black zone in the pie charts indicate the reconstructed proportion of animal matter in the diet in A and the reconstructed proportion of terrestrial habitat use in B on the basis of maximum likelihood. An asterisk indicates taxa that were excluded from maximum likelihood analyses because of missing data (i.e., taxa for which either ecological or external morphological data were unavailable). Terminal taxa are as follows: 1, *Graptemys ernsti*; 2, *Graptemys gibbonsi*; 3, *Graptemys pulchra*; 4, *Graptemys barbouri*; 5, *Graptemys caglei*; 6, *Graptemys flavimaculata*; 7, *Graptemys oculifera*; 8, *Graptemys nigrinoda*; 9, *Graptemys ouachitensis ouachitensis*; 10, *Graptemys pseudogeographica kohnii*; 11, *Graptemys pseudogeographica pseudogeographica*; 12, *Graptemys ouachitensis sabinensis*; 13, *Graptemys versa*; 14, *Graptemys geographica*; 15, *Malaclemys terrapene* (Atlantic Coast subspecies); 16, *Malaclemys terrapene* (Gulf Coast subspecies); 17, *Trachemys decorata*; 18, *Trachemys decussata*; 19, *Trachemys terrapen*; 20, *Trachemys stejnegeri malonei*; 21, *Trachemys stejnegeri stejnegeri*; 22, *Trachemys stejnegeri vicina*; 23, *Trachemys scripta hartwegi*; 24, *Trachemys scripta callirostris*; 25, *Trachemys scripta venusta*; 26, *Trachemys dorbigni*; 27, *Trachemys gaigeae*; 28, *Trachemys scripta cataspila*; 29, *Trachemys scripta ornata*; 30, *Trachemys scripta grayi*; 31, *Trachemys scripta nebulosa*; 32, *Trachemys scripta taylori*; 33, *Trachemys scripta scripta*; 34, *Trachemys scripta elegans*; 35, *Trachemys scripta troostii*; 36, *Pseudemys*

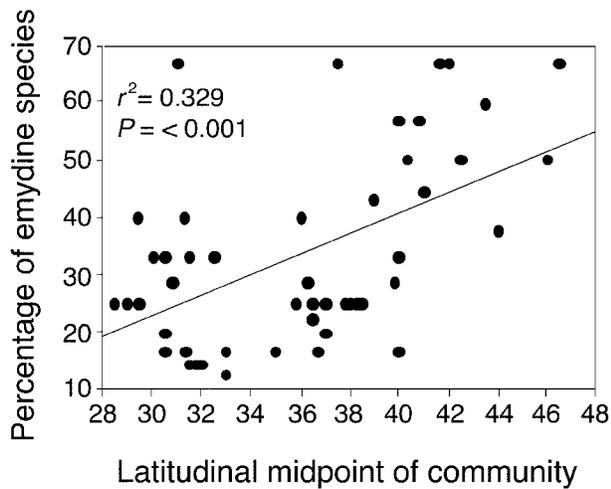


Figure 3: Relationship between the latitudinal midpoint of a community and the percentage of emydid (vs. deirochelyine) species in the community for emydid communities in eastern North America, showing the dominance of northern communities by emydid species and of southern communities by deirochelyines.

statistically supported (i.e., the 95% confidence intervals on the reconstructed ancestral values overlap the values for descendant taxa), but these confidence intervals may not reflect the accuracy of the reconstructions (see “Material and Methods”).

To summarize, seven of the 10 species that are widely distributed in eastern North America occur in >20% of both southeastern and northeastern communities, and all seven of these species show phylogenetically conserved ecological characteristics. On the basis of reconstruction of latitudinal midpoints, all seven of these species seem to occur north of their immediate ancestors, but given that there is an unknown level of uncertainty in each of the reconstructed values, these results can be considered only tentative. Regardless of whether they originated in northeastern or southeastern North America, the ecologically conservative dispersal of these emydid turtles has considerably homogenized patterns of community structure in eastern North America.

Discussion

Our results demonstrate that phylogenetic trends in ecological characteristics can strongly influence regional

trends in the ecological structure of communities. However, whether these phylogenetic trends contribute to similarity or dissimilarity in structure between regions may depend on the extent of dispersal between regions.

Some previous studies have shown a strong imprint of phylogenetic history on patterns of community structure (e.g., Gorman 1992; Cadle and Greene 1993; Price et al. 2000) such that communities in different regions have remained dissimilar over time because different lineages with different ecological attributes inhabit each region. Like previous studies, our study also demonstrates the role of phylogenetic trends in ecology in creating divergent patterns of community structure between regions, primarily manifested in patterns of habitat use between southeastern and northeastern North America (i.e., the preponderance of aquatic deirochelyines in the south vs. semiterrestrial emydines in the north; fig. 4A, 4C).

Previous studies suggest that similarity in community structure between regions is often caused by adaptive evolution of unrelated species to similar environmental conditions (i.e., convergence; Winemiller 1991; Losos 1992; Hertel 1994; Losos et al. 1998). In contrast, our study demonstrates that the effects of phylogenetic history on geographic patterns of emydid community structure are not blurred by convergent adaptive evolution (fig. 1A) so much as by dispersal (fig. 1C). Even when widespread species were included, latitudinal trends in the percentage of aquatic species in communities were clearly related to differences in the taxonomic composition of communities (fig. 4B). However, the correlation between the percentage of aquatic species and latitude was much stronger when widespread species were removed ($r^2 = 0.805$ vs. $r^2 = 0.329$, with all species). In the case of diet, phylogenetic effects on patterns of community structure became apparent only after widely distributed species were removed from consideration (i.e., the correlation between the percentage of emydines and omnivores in communities changed from $r^2 = 0.027$ to $r^2 = 0.797$).

On the basis of trends in the distribution of the species in the two emydid subfamilies (table 1), we hypothesized that patterns of community structure in eastern North America had been homogenized by the recent dispersal of (aquatic) deirochelyines northward and (semiterrestrial and terrestrial) emydines southward. However, reconstructing the latitudinal midpoints of the geographic

nelsoni; 37, *Pseudemys rubriventris*; 38, *Pseudemys alabamensis*; 39, *Pseudemys gorzugi*; 40, *Pseudemys texana*; 41, *Pseudemys concinna*; 42, *Pseudemys peninsularis*; 43, *Chrysemys picta marginata*; 44, *Chrysemys picta picta*; 45, *Chrysemys picta dorsalis*; 46, *Chrysemys picta belli*; 47, *Deirochelys reticularia*; 48, *Terrapene nelsoni klauberi*; 49, *Terrapene nelsoni nelsoni*; 50, *Terrapene ornata luteola*; 51, *Terrapene ornata ornata*; 52, *Terrapene carolina major*; 53, *Terrapene carolina carolina*; 54, *Terrapene carolina mexicana*; 55, *Terrapene carolina triunguis*; 56, *Terrapene carolina bauri*; 57, *Terrapene coahuila*; 58, *Terrapene coahuila nelsoni*; 59, *Emydoidea blandingii*; 60, *Emys orbicularis*; 61, *Actinemys marmorata*; 62, *Glyptemys insculpta*; 63, *Glyptemys muhlenbergii*; 64, *Clemmys guttata*.

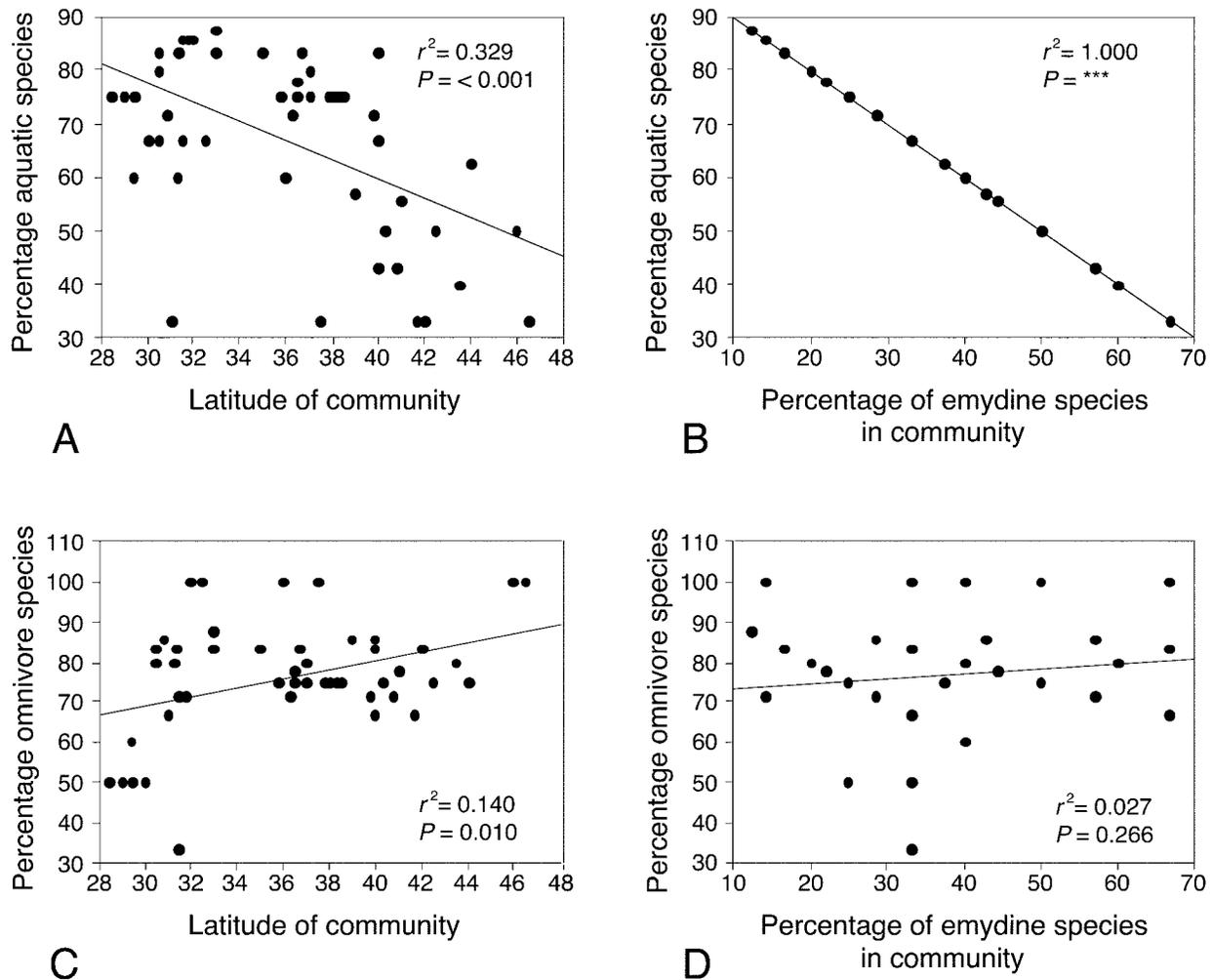


Figure 4: Regional trends in the ecological structure and clade (subfamily) composition of emydid communities in eastern North America

ranges of ancestral emydids suggests that all of the species that are widely distributed in both southeastern and northeastern North America had immediate ancestors that were more southern in distribution (table 1). Rather than being blurred by the exchange of species between two regions (as depicted in fig. 1C), patterns of community structure in eastern North America may have been homogenized by dispersal of several species with conserved ecological characteristics from southeastern communities into the northeast (but see caveats in "Material and Methods"). The dispersal of species into northeastern North America would have added aquatic and terrestrial species to a region that otherwise would contain only semiterrestrial emydines (i.e., *Glyptemys*, *Clemmys*, and *Emydoidea* species) and also would have added dietary specialists (herbivores

and carnivores) to a region that otherwise would have none.

What would account for a pattern of asymmetric dispersal? One possibility is that southern communities are not invulnerable to northern semiterrestrial emydines because of biotic interactions with southern species. It is easy to imagine, for example, that a habitat generalist such as *Glyptemys insculpta* would be unable to invade southern communities that contain species specialized for all the habitats it utilizes (e.g., terrestrial *Terrapene* and aquatic *Pseudemys*). It is also possible that dispersal occurs independently of existing community structure and that northern species are unable to disperse any further south because of phylogenetic niche conservatism (e.g., limited physiological tolerances to warmer climates). Our suspi-

cion is that the latter scenario applies, but we are currently testing these hypotheses.

We conclude that even if lineages are highly conservative in their ecological traits, the effects of phylogenetic history on differences in community structure between regions may be manifested only when there is both phylogenetic conservatism in ecological characteristics and limited dispersal between regions. Previous phylogenetic studies of community structure have generally sampled geographically distant communities (e.g., Richman 1996; Price et al. 2000) or biotas with strong barriers to dispersal between communities (e.g., Losos et al. 1998; Bernatchez et al. 1999). The effects of dispersal will be most apparent when there is comprehensive sampling of communities in a region with few intervening geographic barriers, as in this study. Ecologically conservative dispersal may be an important force in determining patterns of community structure in many continental and oceanic regions.

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